Feeding effects of postlarval red abalone, *Haliotis rufescens* (Mollusca: Gastropoda) on encrusting coralline algae

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Abstract

Detailed examinations of an algal-microherbivore symbiosis have revealed mutualistic components of such herbivore-plant interactions. High-resolution photomicroscopy and experimental analyses in the field and laboratory were used to evaluate effects of foraging by *Haliotis rufescens* (red abalone) postlarvae ~ 200 μm in length, on their encrusting red algal hosts, *Lithothamnion* (=*Lithothamnium*) *californicum*, *Lithophyllum lichenare*, and *Hildenbrandia rubra* (=*H. prototypus*). We have quantified the microscopic food availability, postlarval foraging behaviour, changes in stomach and faecal contents, growth, and mutualistic effects of grazing. Host algae were found to benefit both from a reduction in coverage by epiphytic algae, and from enhancement of vegetative growth.

Introduction

Planktonic larvae of the gastropod mollusc *Haliotis rufescens* Swainson, 1822 (red abalone) are induced to settle and metamorphose specifically upon contact with various species of encrusting red algae (Morse *et al*. 1979; 1980; Morse and Morse 1984). This substratum-specific recruitment of the larvae is induced upon contact with γ-aminobutyric acid (GABA)-mimetic molecules. These molecules, inducing settlement and metamorphosis, are uniquely available to the larvae at the surfaces of encrusting red algae (Morse and Morse 1984). Juveniles of this and several other species of *Haliotis* are found primarily associated with encrusting red algal substrata (Crofts 1929; Shepherd 1973; Morse *et al*. 1979; 1980; Saito 1981; Douros 1985; Hooker and Morse 1985; Shepherd and Turner 1985; Shepherd and Daume 1996), and the larvae of 13 different species of *Haliotis* have been shown to settle and metamorphose specifically in response to encrusting red algae, extracts of these algae, the purified GABA-mimetic compounds, or GABA (Morse 1984; 1992; 1994).

The symbiotic interaction between *Haliotis* and the recruiting crustose red algae has been suggested to be mutualistic, with reciprocal advantages to both the plant and animal (Morse *et al*. 1979; 1980; Morse and Morse 1984; Morse 1992). The advantages to the animal have been discussed and documented previously (Morse *et al*. 1980; Morse and Morse 1984; Morse 1994). What is more difficult to establish is the possible benefit that might accrue to the host algae. Adey (1973) and Steneck (1982) have shown that a particular encrusting red alga, *Clathromorphum circumscriptum*,

is dependent upon the grazing action of adult *Acmaea testudinalis* limpets, which often settle as larvae and remain associated with their encrusting algal host (Steneck 1982). In the case of *Haliotis*, however, these molluscs initially settling on encrusting red algae typically are mobile, remain in coralline habitats until the abalone are ~ 6 mm in length (Shepherd and Daume 1996), but leave these substrata as they grow. Adult abalone then become more common in rock crevices, where they feed on various foliose algae (cf. Cox 1962; Hooker and Morse 1985). If the association between *Haliotis* and the encrusting red algae is directly advantageous to the algae, such benefits must accrue while the haliotids are young and still associated with their initial algal host. We report here experimental data that support the hypothesis that small *Haliotis rufescens* postlarvae, soon after settling onto crustose red algae, can in fact both decrease epiphytic overgrowth and enhance vegetative growth of their host algae in a mutualistic symbiosis, before the molluscs grow to larger sizes. Such influences of small postlarval organisms in natural communities rarely have been considered.

Materials and Methods

Haliotis rufescens and its encrusting algal substrata were collected from shallow subtidal areas off Santa Barbara, California. Larvae and juveniles were raised in the laboratory as described previously (Morse *et al.* 1979; 1980). Following cultivation of the lecithotrophic larvae for 7–10 d at 15 °C, settlement and metamorphosis on encrusting red algal substrata were induced by exposure of the developmentally competent, swimming larvae to suitable algae-encrusted rocks for 0.5–1 h (Morse *et al.* 1979; 1980). Postlarvae were studied throughout their growth from settlement (at a shell length of ca. 200 μm). Larger juveniles and broodstock of *H. rufescens* were collected from the field.

Small rocks of igneous and metamorphic mineral composition (<250 g each) were collected from tide pools near Santa Barbara, California, where they were common both in tidal pools and subtidally. Rocks were selected that were encrusted primarily with the common coralline red algae *Lithothamnion* (=*Lithothamnium*) *californicum* and *Lithophyllum lichenare*, and the uncalcified encrusting red alga, *Hildenbrandia rubra* (=*prototypus*). Algae were identified according to Abbott and Hollenberg (1969; 1976), with assistance and advice from I. Abbott, G. Hollenberg, and R. Steneck (pers. comm.). Rocks encrusted with these algae are common in shallow subtidal habitats of postlarval *Haliotis rufescens* (Morse *et al.* 1980), and can be used experimentally (Morse and Morse 1984) for studying *H. rufescens* settlement, metamorphosis, and grazing.

Laboratory Observations

At 2–3 d intervals following metamorphosis, at least five groups of abalone on different rocks were observed as described below, and their activities tabulated. Submerged algae and molluscs were viewed clearly by placing a microscope cover slip on the water's surface film. A Zeiss 16-mm objective lens with iris provided a long working distance and depth of field, at 80X–160X on a compound microscope, or at 10X–100X with a 35-mm camera and bellows. A halogen fiber-optic illuminator used at <1/10 maximum output in a darkened room provided cool, focused illumination for observations. A focused, high-speed electronic flash unit (Zeiss) provided photographic illumination at ca. 1/5000 sec.

Field Observations

Quantitative, high-resolution field experiments testing the impact of microscopic *H. rufescens* grazers, begun May 4, 1979, were completed with three matched pairs of algae-encrusted rocks roughly 5 cm in diameter. Pairs were matched as closely as possible for algal patch shapes and sizes. Two pairs (for replication) of the rocks had live encrusting algae; a third pair (without replication here) had encrusting algae killed by boiling ("no live encrusting algae," below). These substrata were suspended from a floating wharf in outer Santa Barbara Marina, with monofilament fishing line (0.5 mm diam.) tied around the center of each rock. These rocks were suspended at a depth of 40 cm,

approximately 15 cm apart. Their order in the row was changed frequently during the experiment to minimize any subtle differences in physical environments. Additional rocks (treated as those described above) for further replication were lost during the experiment, although their less complete sampling yielded additional qualitative results. Later supplementary observations of the rocks remaining 4 mo and 12 mo after the start of the experiment showed that the encrusting algae survived in this environment. Each of the algal species also occurred on adjacent cement floats during the experiments.

In these experiments, larval *H. rufescens* were settled periodically on the algae by placing the rocks in a container of competent larvae (500-ml volume; 40 larvae/ml) for 30 min in the field. Every 4 days for over 2 mo, *H. rufescens* was restocked this way consistently on two of these rocks (from two pairs, each with one rock selected arbitrarily at the beginning of the experiment) while the other four rocks received no molluscs. These four rocks were placed in a container of laboratory seawater while the other two rocks were being restocked in the container with larvae, thus controlling for any effects of the treatment. Swimming animals such as potentially grazing amphipods would have had equal access to each rock, but only twice was an amphipod seen on the rocks during the observations. Each rock used had at least five well-separated patches of *Lithothamnion californicum* on each side; these provided at least five pseudo replicates (or subsamples) on each side for quantitative microscopic analyses. (Statistics therefore compared experimental pairs of rocks, with duplicate rocks for the presence of grazers, rather than attempting to compare rocks in general.)

At two-week intervals, photographs were taken in the field with a 55-mm micro lens for 0.25 X photographs, and with additional extension tubes for 1.5 X photographs. The camera's micrographic reticle focusing-screen enabled viewing a clear image at 1.5 X, for focusing on the center of each rock surface. A 10x13-cm photographic glass plate (stripped of emulsion with hypochlorite bleach) flattened the rippled water in the pan of rocks being photographed; the plate was cemented inside a wooden frame, which served as a float.

The resulting Kodachrome transparencies were scored for algal abundances by viewing them with diffuse light under a dissecting microscope at 20X. Percentage cover of epiphytic algae overlying the encrusting red algal substrata was determined by a point-intercept method. Five microscope fields sampled at random were scored with an ocular micrometer grid to compute cover of epiphytic (filamentous) algae, based on >120 grid points actually intercepting the algae (after Kitting 1980). Similarly, densities of epiphytic algal filaments were counted in five separate 60X views; these defined five fields (each 12 mm^2) as microscopic quadrats on each rock at each sampling time. Evidence for expansion of the encrusting algal substrata was sought in the close-up photographs. Such growth could be assessed clearly on the monofilament line only, as this line extended around each rock and delineated a clean spatial boundary of known age. Expansion of each alga onto a line was scored as percentage encrustation along the length of line that extended over the alga. Data analysis was performed with the use of Sokal and Rohlf (1969), restricting statistical conclusions to the actual rocks in the experiment. Due to small sample sizes remaining throughout the field experiment, direct observations were necessary to strengthen conclusions. Thus, each of these field experiments was supplemented with subsequent laboratory and field observations of postlarvae and freshly collected algae in flowing seawater.

Results

Initial Abundances of Microscopic Epiphytic Algae

Miniature 1 mm x 1 mm quadrats examined in microscope fields at 200X showed sparse epiphytic algae available on freshly collected algae-encrusted rocks; most epiphytic algae were concentrated where coralline algal patches abutted. Naviculoid diatoms were most common, in densities up to 50/mm^2 on live encrusting algae. Cocconeid diatoms reached a maximum of 30/mm^2. Cyanobacteria and green and red filamentous algae were far fewer. Total microscopic algae together with

Table 1.   Summary of observations on feeding of postlarval *Haliotis rufescens* on crustose coralline red algae. All material was maintained at 15°C in flowing filtered seawater. Each observation noted is based on at least three (and usually >5) individuals observed in each manner, on freshly collected *Lithothamnion californicum*. Brackets indicate data are unchanged throughout those ≥2 time periods.

Parameter	Age Post-Metamorphosis (days)					
	0	1–6	10	13	20	45
SHELL LENGTH (mm)	0.20	–	0.25	–	0.50	1.0
MOBILITY	[	10 shell lengths per 37±11 sec	]	<100 shell lengths per day (net)		sedentary
RADULAR MOTION	initially in sac	[smooth sweeping	]	[forceful scraping		]
MEAN NUMBER OF FEEDING MOTIONS (per sec) (intermittant)	[	0.63 – 0.80 (continuous)	]	0.80 – 1.3 [(irregular)	0.80 – 1.1]	1.3
RADULAR WEAR	[	none	]	slight on 2 rows of teeth	on 2 rows	on 4 rows
STOMACH CONTENTS (whole mounts of postlarvae)	velum?	[no solids	]	cyanobacteria plus diatoms		coralline algal cells, cyanobacteria, diatoms
FECAL CONTENTS	[	no solids	]	CaCO₃ fragments smaller than algal cells (<5 μm diam)		CaCO₃ fragments larger than algal cells (>5 μm diam)

cyanobacteria represented <2% cover, as sampled with point intercepts with an ocular micrometer grid. Even fewer visible epithallial flakes from the coralline algae were seen, but thin, clear algal mucus was observed to be widespread.

Early Post-Settlement Feeding Behavior

Table 1 summarizes our observations of feeding behavior of the smallest *H. rufescens*. Immediately after we allowed the larvae to settle and metamorphose on each of the encrusting algal substrata, these smallest postlarvae moved their shells and mouths very actively, but cellular solids were not eaten detectably for the first 10 days. During this period, juveniles were very active as their shell length increased from about 200 µm to 250 µm (Fig. 1A). During the first 10 days following metamorphosis, postlarvae traveled about 0.3 shell lengths/sec. The mouth glided quickly, smoothly, and almost continuously over the encrusting algal surface. Some of the mucus on the algae (cf. Morse *et al.* 1980), detectable via adhering microscopic debris, was swept toward the mouth during this activity.

At 10 d post-metamorphosis, ten individuals timed for the interval required for 20 consecutive mouth motions swept their mouths over the algae at an average rate of 0.63 ± 0.21 (S.D.) times per sec. No visible solids appeared in the feces or stomach, viewed in whole mounts of the animals at 1000X. Any bacteria in the stomach or on available algae were too sparse to be detected; bacteria were visible only in additional preparations of damaged, moribund postlarvae, possibly infected or beginning to decompose. Fresh preparations, pressed to expose the radula, revealed at least four rows of well-formed teeth on the radula, with no observable wear even on the oldest teeth (after Kitting 1980) viewed at 1000X (Table 1).

At 12–15 days post-metamorphosis, juvenile feeding became more intermittent, forceful, and less smooth over the algae (Table 1). Ten timings of 20 consecutive mouth motions showed an average of 1.04 ± 0.16 (S.D.) motions/sec. Several intact but damaged (without normal pigmentation) cyanobacteria, small diatoms (~5 µm long), and fragments apparently derived from the coralline algae were found in the stomachs and in fecal pellets (10 x 50 µm; e.g., Fig. 1B) viewed at 1000X. Radulae showed two noticeably worn lateral teeth of the six well developed ones (Fig. 1C). This feeding by distinct scraping continued at least until 60 days following metamorphosis.

Continuing observations of *H. rufescens* juveniles as they grew showed that they became largely sedentary after 20–45 days post-metamorphosis, when the juveniles had reached a shell length of almost 1 mm. By this time, whole cells from the encrusting red algae appeared in stomachs (viewed in whole mounts), and at least four rows of radular teeth showed wear when examined as above.

Effects of Populations of Small Grazers on the Growth of Epiphytic Algae

Each group of *H. rufescens* introduced to the suspended rocks disappeared after 4–8 days; postlarvae were observed (in pans in the field) to be dislodged from occasionally swaying substrata. Furthermore, those larvae and postlarvae among dense erect red algae (e.g. *Acrochaetium*) on such rocks often were consumed by associated terebellid polychaete worms. Restocking of the molluscs every 4 days on the suspended rocks thus maintained postlarvae <8 days old, with almost all <4 days old. Counts of postlarvae before and after each restocking showed an overall population density of roughly 7 individuals/cm².

Frequent direct observations, and photographs of experimental and control rocks at two-week intervals, showed noticeable differences in epiphytic algal growth between these rocks with postlarvae and those without. Filamentous epiphytes appeared gradually over the rocks, especially those without postlarvae (Figs. 2A,B,C), although all rocks initially had appeared relatively clean and smooth. The epiphytic cover consisted primarily of a filamentous green alga, *Enteromorpha flexuosa*. Microscopic analyses in the field revealed that after seven weeks, the numerous patches of the encrusting coralline alga *Lithothamnion californicum* on the two rocks with abalone, had less than half the density of filamentous algae covering the *L. californicum* on each matched rock without postlarvae (Fig. 3A; cf. Figs. 2A,B). Pairs of rocks varied somewhat in crustose algal patchiness, and resulting epiphyte
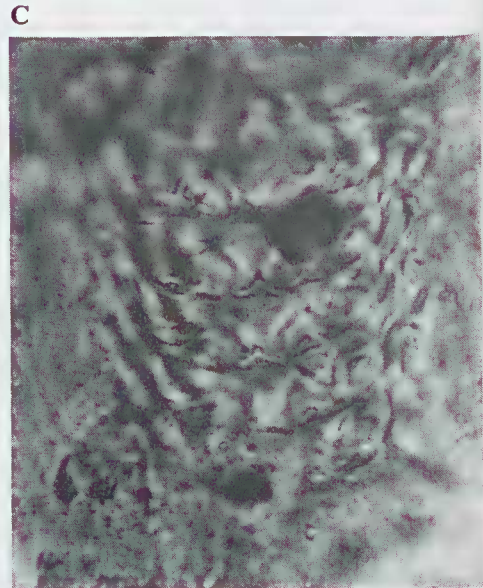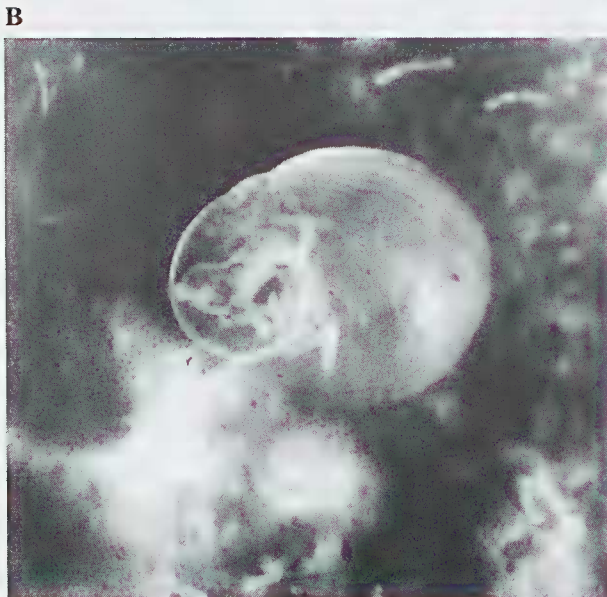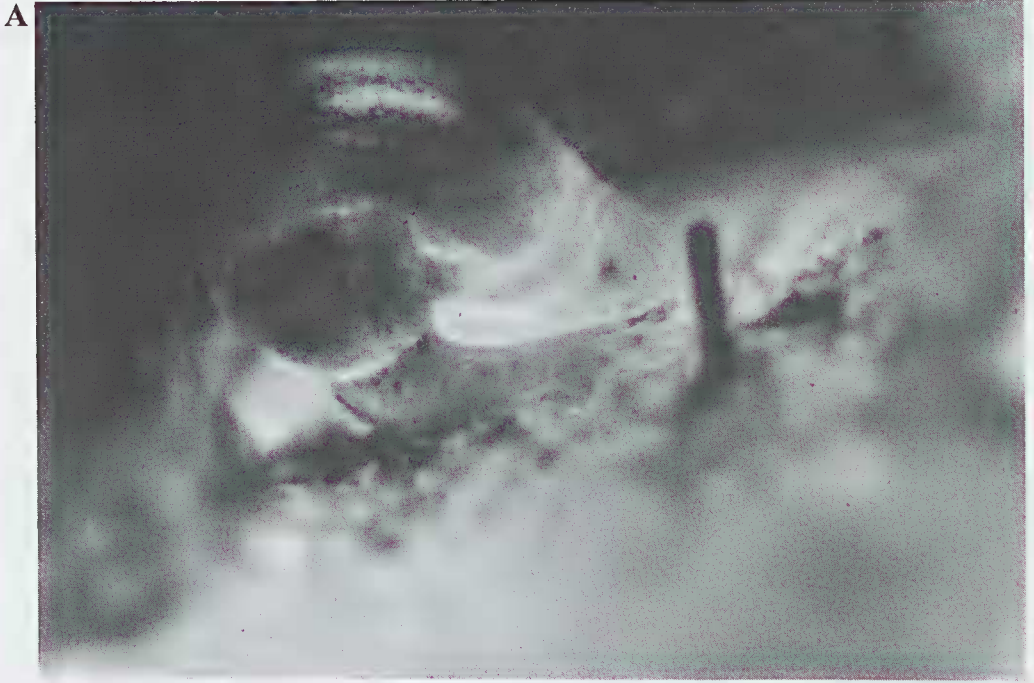
Figure 1.   Feeding by postlarval *H. rufescens*. A. Anterior view of an individual 4 days post-metamorphosis on a coralline alga, with 3-celled green algal filament to right and a bryozoan zooid to left. Photographed area is 500 μm long. B. Dorsal view of 25-day post-metamorphic individual with fecal pellets on coralline algal substratum. Shell length ca. 600 μm. C. Compound microscope view of the radula of a 12-day post-metamorphic individual, in a whole-mount of the animal. Distal working end is lowest, with the lowest pair of the six discernible lateral teeth noticeably rounded from wear. (Long slender marginal teeth are less discernible.) Unidentified fragment is visible at upper right on the radula. Radular width ca. 50 μm.

filaments extending from adjacent patches of rock. However, considering mere pseudoreplication of algal patches on each rock, and only two grazer replications remaining throughout the field experiment, the overall density of epiphytic algal filaments on this coralline alga (specifically on these rocks) indicated a statistically significant difference in the presence and absence of the postlarval molluscs (one-way ANOVA; $F = 26.7$, $df_1 = 1$, $df_2 = 2$, $P < 0.05$). The difference in percentage cover of filamentous algae on coralline algae (Fig. 3B) also became noticeable after about five weeks, and was statistically significant (G-test on all raw data, not percentages, after five weeks; $G = 72.4$, 1df, $P < 0.005$).

Coralline algae themselves also appeared to deter colonization by epiphytic algae on these rocks. Coralline algae on rocks without abalone had less than one-fifth the density of algal filaments observed on the rocks having no live encrusting algae or postlarvae (Figs. 3A,B; cf. Fig. 2C); these differences appeared highly significant statistically after seven weeks for both filament counts and percentage cover (ANOVA and G-test, respectively; $P < 0.005$).

The numerous patches of the encrusting uncalcified alga *Hildenbrandia rubra* on the two rocks with abalone also had much lower percentage cover of filamentous algae after about five weeks, compared with the *H. rubra* on the pair of rocks without postlarvae (Fig. 3C; G-test on raw data; $P < 0.005$). In each statistical comparison itself, minimal replication limits generalization, but supplementary qualitative observations often were more conclusive, and consistent with the quantitative data. The dark color of the *H. rubra* (not calcified) prevented reliable counts of individual epiphytic filaments overlying this species, but the epiphytes also appeared to be more dense on the ungrazed *H. rubra*, as they were on the *L. californicum* quantified above. Although the second coralline alga, *Lithophyllum lichenare*, was not sufficiently abundant in our samples to allow quantification of its epiphytes, subjective observations suggested that it, too, had fewer epiphytes when grazed by the postlarval gastropods than when ungrazed.

Effects of Populations of Small Grazers on Coralline Algal Growth

It was necessary for these studies to obtain an index of encrusting algal fitness that might reflect effects of grazing or epiphytism. No significant changes in the density of conceptacles (encrusting algal reproductive structures) nor overall sizes of the crusts were observed during the course of our experiments. However, the systematic close-up photographs revealed clearly quantifiable and significant differences in the vegetative growth of these coralline algae over the introduced surfaces of monofilament line (cf. Fig. 2). This growth clearly was noticeable only in the presence of the postlarval *H. rufescens* (Tables 2 and 3). The monofilament line remained secure around each rock, presenting an inert boundary over which algal growth could readily be detected accurately. Quite consistent results were observed (Table 2); after the third week of the experiment, the grazed

Table 2. Effects of postlarval grazing on the vegetative growth of coralline red algae. Summary of observations, taken by point-intercept method (from 1.5-X photographs), for coralline algal growth over monofilament line, with and without postlarval *H. rufescens* during weeks 3–6. Statistical significance (among subsamples and minimal replication) is presented in the text.

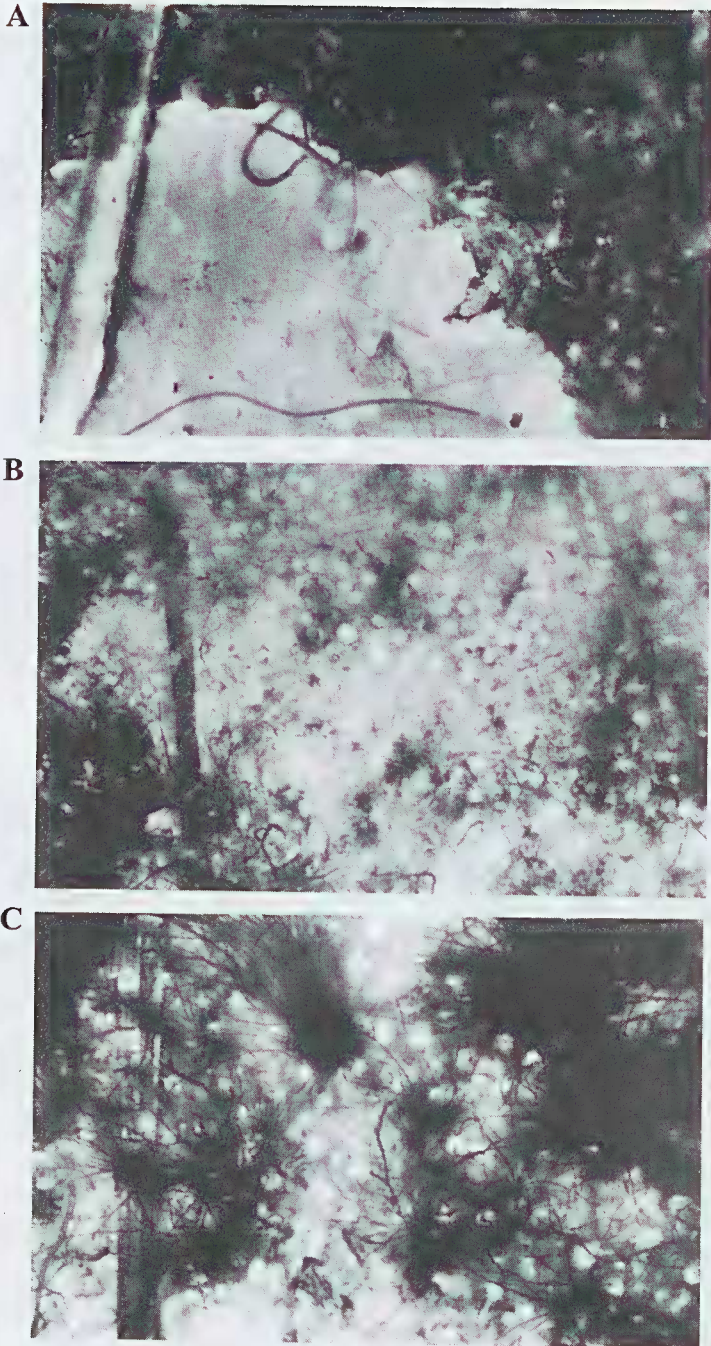| Alga	*H. rufescens* present	Portion of algal monofilament transect overgrown	
		(points overgrown/ total points scored)	(percentage)
Lithothamnion	Yes	24 / 60	40%
"	No	0 / 84	0%
Lithophyllum	Yes	29 / 65	45%
"	No	0 / 20	0%

Figure 2.   Effects of postlarval grazers on crustose red algae, after 4 weeks of the experimental regime. Each representative photographed area is ~5 mm high (cropped from 1.5X photographic samples). Monofilament line extends over algae near the margin of each photograph. Filamentous green algae overgrow scattered areas. A. Live encrusting algae with average density of *H. rufescens*. Five oblong individuals (<4 d post-metamorphosis) are visible. Coralline algal growth over line is beginning. Two weeks later, coralline growth over the line extended all along each side of the line. B. Corresponding sample of rock without molluscs. C. No live encrusting algae nor molluscs.

Table 3. Effects of postlarval grazing on the vegetative growth of coralline red algae. Summary of observations, for *Lithothamnion* and *Lithophyllum*, by algal patch. Other details as in Table 2 and Methods. G-test on raw data (among patches) indicates statistically significant differences among these rocks, at P < 0.01.

| Postlarval *H. rufescens* present | Coralline algal patches overgrowing monofilament | |
	(patches overgrowing line/ total patches)	(percentage)
Yes	15 / 23	65%
No	0 / 33	0%

Lithothamnion californicum was overgrowing the monofilament line along 40% of the line overlying this crust (measured by the point-intercept method); grazed *Lithophyllum lichenare* similarly showed 45% overgrowth of the line. In marked contrast, the coralline algae on ungrazed rocks showed no detectable overgrowth of the line in any of the possible instances observed (Table 2). For each of these two algae, the differences observed in such growth in the grazed samples versus ungrazed controls were statistically significant (three G-tests on raw data; P <0.01).

A similarly significant effect of postlarval *H. rufescens* is seen in the percentage of coralline algal patches showing enhanced vegetative overgrowth (Table 3). However, neither grazed nor ungrazed *Hildenbrandia rubra*, which had a slower growth rate than the coralline algal species studied, ever was seen to grow over the monofilament line in any of the >20 instances observed in these experiments.

Discussion

Postlarval Feeding on Encrusting Algae

Our detailed analyses of encrusting algae show small-scale but detectable effects of postlarval grazing; young gastropods recruited onto the encrusting algae evidently can help decrease epiphytic overgrowth and increase coralline host algal growth soon after the gastropods settle. At least under relatively calm, shallow-water conditions, even the youngest molluscs settling there (<4–8 days post-metamorphosis) appeared to influence the algal surface, as seen in our quantitative experiments in the field, and in our qualitative observations in the laboratory. The average experimental density of about 7 individuals/cm² is probably higher than the densities of juvenile *Haliotis* spp. usually occurring in the natural environment. Morse *et al.* (1980) found overall densities of larger individuals of *Haliotis* spp. (1–22 mm long) to be over 2.2 individuals/100 cm² of bottom; they were concentrated on patches of encrusting algae. Our experimental density may approach naturally occurring densities of total postlarval grazers (of several species) settling on such algal patches. Larvae of a number of other grazing species of chitons (Barnes and Gonor 1973; Morse *et al.* 1979) and gastropods (*e.g.*, Heslinga 1981; Steneck 1982) have been observed to settle and metamorphose preferentially on encrusting red algae. Juveniles of a number of species of *Haliotis* (e.g., Crofts 1929; Shepherd 1973; Saito 1981; Morse 1984; Hooker and Morse 1985), limpets (Morse 1980; Steneck 1982), starfish (Barker 1977), and other invertebrate grazers (see Morse *et al.* 1980) also occur preferentially on these encrusting algae; hence, postlarval foraging activity on these encrusting algal substrata may be high. Even though postlarvae may not initially graze host or epiphytic algal cells directly, their active shell movements and disturbance to surface algal mucus appeared to decrease epiphytic algal buildup. Our analyses of microscopic quadrats showed that these algal surfaces possess, in addition to algal mucus, sparse and patchy microscopic algae and epithallial coralline algal fragments, which can be consumed by larger juvenile grazers such as *H. rufescens* >10 days after metamorphosis.
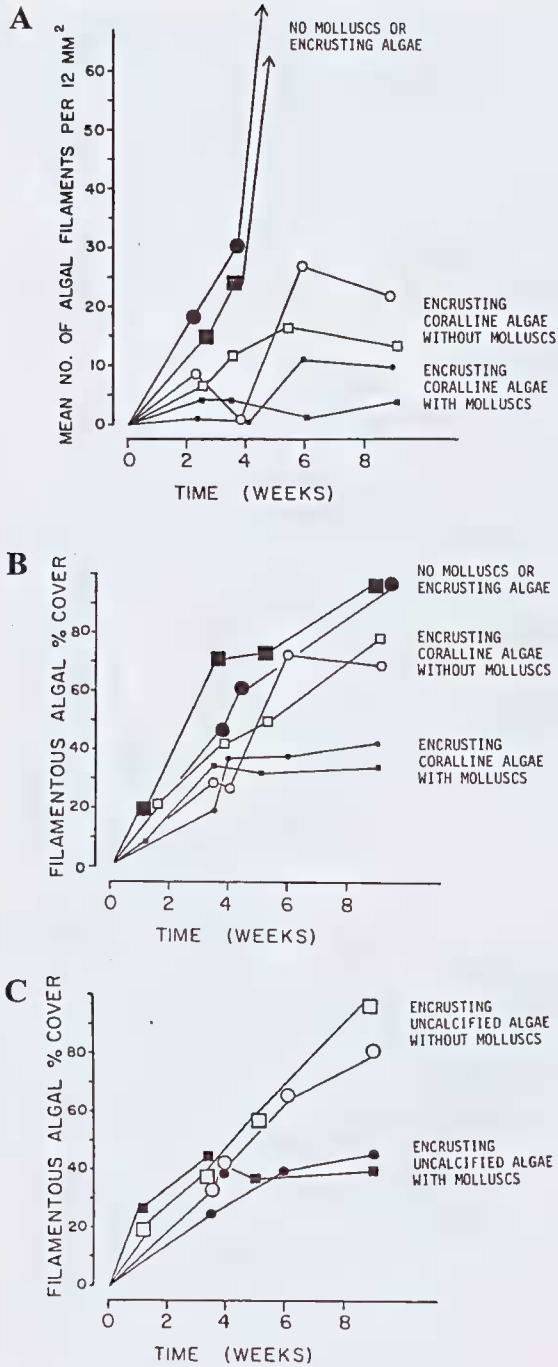
Figure 3.   Quantification of epiphytic growth on encrusting algae on each side of experimental rocks. More than five replicate patches of *Lithothamnion* (in Fig. A and B) and *Hildenbrandia* (in Fig. C) were present on each side of a rock. Squares = one matched pair of sides, circle = other matched pair. Open versus closed symbols represent different treatments (as labeled on Figure). Fig. A includes bars as ±1 standard error (among algal patches as subsamples). Data are scored by point-intercept method, as described in Methods. Symbols on Figs. B and C approximate the size of error bars (*i.e.* ± <5%, again among algal patches as subsamples).

The youngest *H. rufescens* demonstrated active foraging behavior with very rapid mouth movement, yet without any detectable particles appearing in their stomachs for the first 10 days of postlarval growth. The rapid, smooth movements of the mouth parts, lack of visible radular wear, and lack of feces all suggest that little scraping occurs in this early feeding stage, but that the youngest juveniles may instead be deriving nourishment from the glycoprotein mucus exuded from the encrusting algal substratum (Morse *et al.* 1980). Associated microorganisms then may become important quickly, since very young abalone in culture grow more quickly on certain unicellular foods than on clean coralline algal surfaces (Hooker and Morse 1985). Young *H. rufescens* also can survive and grow for at least one week following metamorphosis, nourished only by endogenous reserves of yolk and occasionally by ingestion of yolk-rich cells of the velum (the larval swimming organ shed at metamorphosis; Morse 1984; Hooker and Morse 1985; cf. Fretter 1972). Thus, little if any damage to the encrusting host alga need result from the initial colonization by the postlarval *H. rufescens* recruits.

Coralline *Lithothamnion* and *Lithophyllum*, and the tough uncalcified *Hildenbrandia* tissues all were rasped extensively by juvenile *H. rufescens* several weeks old. Adey (1973), Steneck (1982), and Kitting (1984a) found that other gastropods, as small adults, rasped encrusting coralline and tough uncalcified algal species extensively. Future close observations may show that seemingly tough encrusting algae often are browsed by relatively inconspicuous rasping by various small animals.

Mutualistic Symbiosis

Results of the experiments presented here indicate that the symbiotic relationship between encrusting red algae and their associated small molluscan grazers can, in fact, be mutually beneficial to the plant and animal partners. In the case of *H. rufescens*, such mutualistic benefits can be detected during the early period in which the larvae settle and metamorphose, and postlarvae begin to grow on their host algae. As discussed previously, this association benefits the recruited *Haliotis* by providing specifically required morphogenetic inducers that are uniquely available at the surfaces of encrusting red algae (Morse and Morse 1984), and by provision of suitable physical environments, sources of nutrition, and camouflaging pigmentation (Morse *et al.* 1979, 1980; Morse and Morse 1984). Steneck (1982) pointed out the suitability of relatively smooth, extensive coralline algal surfaces for firm attachment by small molluscs such as limpets, and Littler and Littler (1984) showed that another *Lithophyllum* sp. can indicate locations that experience constant immersion and little physical disruption. In addition, our supplementary observations of postlarve placed on freshly collected rocks show that encrusting algae provide a partial refuge from small polychaete worms and other minute predators, which are more concentrated in sediments or foliose and filamentous algae than on the encrusting red algae. A similar refuge effect has been observed for newly settled larvae of *Astraea undosa* (Markell and Morse, in prep.), and for various sessile invertebrates excluded from patches of filamentous algae by herbivorous fishes (Day 1983). However, when numerous large grazers occur on encrusting coralline algae (see Steneck 1983), the refuge afforded by these algae may be reduced.

The encrusting algal hosts appear to derive reciprocal benefits from *H. rufescens* postlarvae (cf. Morse *et al.* 1980; Morse and Morse 1984). Our observations show that these juvenile molluscs can significantly decrease epiphytic overgrowth of the encrusting algae (Figs. 2, 3), and dramatically increase coralline algal growth onto an open (monofilament) surface, at least under the conditions described (Tables 2, 3). These findings provide evidence that the postlarval molluscs can confer benefits to the encrusting algae, particularly when larval recruitment is high (yielding ~ 7 postlarvae / cm^2).

Likely detriments to the host alga due to epiphytic overgrowth include accumulation of entrapped sediment and detritus, shading when light is dim, reduction in nutrient and gas exchanges, and suppression of growth by potentially allelopathic epiphytes (after Fletcher 1975). Larger grazers have been reported to remove competing algae and augment the growth of various encrusting algae (e.g. Paine and Vadas 1969; Adey 1973; Vine 1974; Wanders 1977; Slocum 1980). However, epiphytes

do not in general kill encrusting coralline algae in instances where light and nutrients are sufficient underneath the epiphytic cover (Vance 1979) nor when coralline algae slough off enough tissue (Johnson and Mann 1986) or have an overlying canopy of algae (see Figueiredo *et al.* 1996).

Adey (1973) and Steneck (1982; 1983) showed that grazing by larger gastropods can benefit a specific encrusting alga by scraping the alga free of dead epithallial tissue and epiphytic overgrowth. Our supplementary field observations suggest that larger individuals of *H. rufescens* do not decrease epiphytic overgrowth of the host alga noticeably; juveniles 1–3 cm in shell length became sedentary in depressions and maintained a clearing free of epiphytes only about the size of their shell (Kitting, unpublished observations).

Our experiment comparing epiphytic overgrowth on live encrusting algae to that on dead algal surfaces (cf. Figs. 3A,B), and analogous larger-scale experiments (Breitburg 1984) show that these encrusting algae resist epiphytic fouling rather effectively in nature, even in the absence of noticeable grazing by macroscopic herbivores (see Figueiredo *et al.* 1996). One mechanism appears to be the sloughing of algal surface tissues, dislodging epiphytes (Giraud and Cabioch 1976; Adey 1973; Johnson and Mann 1986; Keats *et al.* 1994). Another mechanism might involve the action of common microscopic grazers; such small grazers as microscopic postlarvae are not excluded by cages, nor quantified in most grazing experiments. Such microscopic juvenile invertebrates often might be sufficiently common to help keep encrusting algae clean, even where these algae (upon superficial examination) appear to be ungrazed. This suggested significance of microscopic events on encrusting algae contrasts with previous descriptions of encrusting (coralline) algae as simply "primary space" suitable for colonization by other sessile organisms (e.g. Dayton 1971) or "barren grounds" (e.g. Lawrence 1975) within assemblages of larger organisms.

Mechanisms by which postlarval *H. rufescens* grazers contribute to enhanced growth of the coralline algal hosts (Tables 2, 3) are not yet clear. The extension of the grazed algae over adjacent bare (monofilament) surfaces clearly is vegetative growth. No effect on sexual reproduction, or on the microscopic appearance of the algal conceptacles, could be observed. Possible transport of algal cells or propagules by the browsing molluscs (after Kitting 1980; 1984b on larger gastropods) also might have enhanced encrusting algal accumulation, although a direct test of this possibility was negative with young *H. rufescens* (Hooker and Morse, unpublished observations). Fletcher (1975) has reported experimental evidence demonstrating that filamentous algal epiphytes can suppress the growth of encrusting red algae by allelopathic (chemical) means. It thus is possible that the action of small molluscan grazers can enhance growth of their crustose algal hosts (cf. Tables 2, 3, and Fig. 2) by reducing allelopathic suppression by epiphytes.

A model by Roughgarden (1975) demonstrates how commensalism could evolve into mutualism through increased fitness of colonists, which otherwise could evolve to avoid the symbiosis. We suggest additional factors which may help account for reportedly numerous examples of mutualism. Examples of host organisms evolving to rely partially on (possibly diverse) symbiont colonists (e.g. for removal of epiphytes; cf. Adey 1973), as evident for new colonists (postlarvae) in the present study, suggests the importance of evolution of the host, in contrast to the emphasis on the symbiotic colonist in previous models of the evolution of mutualism (Slatkin and Maynard Smith 1979). These various encrusting red algal hosts may benefit from the settlement of various grazing symbionts while resisting damage from these symbionts. We hypothesize that mutualism often may evolve from adaptations of host species to benefit from the presence of otherwise commensal symbionts.

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